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Savanna woody encroachment is widespread across three continents

Running head: Global savanna encroachment

Nicola Stevens^{1,2*}, Caroline E.R. Lehmann³, Brett P. Murphy⁴ and Giselda Durigan⁵

1 South African Environmental Observation Network (SAEON), Fynbos Node, Cape Town, South Africa.

2 University of Stellenbosch, Department of Botany and Zoology, Private Bag X1, Matieland, 7602,
Stellenbosch, South Africa. nicolastvns@gmail.com. Tel: +27 21 808 3236; Fax: +27 21 808 2405

3 School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, United Kingdom

4 Research Institute for the Environment and Livelihoods, Charles Darwin University, Darwin NT 0909,
Australia

5 Floresta Estadual de Assis, Instituto Florestal, 19807-270 Assis, SP, Brasil

** Corresponding author*

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Abstract

Tropical savannas are a globally extensive biome prone to rapid vegetation change in response to changing environmental conditions. Via a meta-analysis, we quantified savanna woody vegetation change spanning the last century. We found a global trend of woody encroachment that was established prior the 1980s. However, there is critical regional variation in the magnitude of encroachment. Woody cover is increasing most rapidly in the remaining uncleared savannas of South America, most likely due to fire suppression and land fragmentation. In contrast, Australia has experienced low rates of encroachment. When accounting for land-use, African savannas have a mean rate annual woody cover increase two and a half times that of Australian savannas. In Africa, encroachment occurs across multiple land uses and is accelerating over time. In Africa and Australia, rising atmospheric CO₂, changing land management and rainfall are likely causes. We argue that the functional traits of each woody flora, specifically the N-fixing ability and architecture of woody plants, are critical to predicting encroachment over the next century and that African savannas are at high risk of widespread vegetation change.

Introduction

The savanna biome covers around 20% of the Earth's surface, contributing 30% of terrestrial net primary production (NPP) (Grace *et al.*, 2006), and is increasingly considered critical to the regulation of the terrestrial carbon cycle (Poulter *et al.*, 2014; Liu *et al.*, 2015). However, savannas are also home to 20% of the Earth's population and the majority of rangelands and livestock (Scholes & Archer, 1997). Understanding current trends in vegetation change across the biome is critical to predicting the future of this ecologically, economically and culturally important biome.

Global change is increasingly understood to be affecting tropical vegetation at large spatial scales. A poorly resolved global driver of vegetation change is the exponential increase of atmospheric CO₂ concentration, henceforth denoted as [CO₂]. Rising [CO₂] affects plant growth and vegetation both directly, and indirectly via [CO₂]-driven climate change (Leakey *et al.*, 2009). Concurrently, humans have caused extensive change in the spatial processes of fire and mega-herbivory that maintain savanna ecosystem function, via land clearing for agriculture, building of roads and fences, hunting, and deliberate lighting or suppression of fire (Lamprey & Reid, 2004; Archibald *et al.*, 2013). Combined, the degree of human-induced land use and land cover change, increases in [CO₂] and future climate change mean change in savanna vegetation structure and function must be anticipated. However, estimates of future savanna vegetation change vary considerably; some modelling studies predict that elevated [CO₂] will drive large increases in savanna woody cover (Higgins & Scheiter, 2012; Donohue *et al.*, 2013), while other models that only consider climate changes produce variable predictions ranging from savannas remaining stable (Bergengren *et al.*, 2011) to savannas invading forests (Anadon *et al.*, 2014) and forests invading savannas (Zelazowski *et al.*, 2011).

Woody encroachment, the increase in woody biomass, stem densities or woody cover, is a symptom of an alteration in ecosystem processes; it has been documented across continents and

biomes (Myers-Smith *et al.*, 2011; Murphy *et al.*, 2014; O'Connor *et al.*, 2014). However, as an open-canopied tropical biome, savannas appear particularly vulnerable to woody encroachment (Parr *et al.*, 2014), where encroachment can have negative consequences for soil carbon storage (Berthrong *et al.*, 2012), ground water recharge, tourism (Gray & Bond, 2013), grazing potential (Angassa & Baars, 2000) and biodiversity (Ratajczak *et al.*, 2012).

Predicting woody encroachment across savannas is hampered by their ecological complexity as a wide range of drivers can act to release constraints on woody plant growth and recruitment – including browsing, grazing, fire, climate, and [CO₂]. Combinations of local (e.g. land use), regional (e.g. changing temperature, rainfall, evaporative demands) and global drivers (e.g. rising [CO₂]) are all recognised as potential causes of increasing woody cover in savannas (Bond & Midgley, 2012). Local land use such as heavy grazing and consequent reductions in fire frequency and intensity promotes encroachment by releasing woody plants from grass competition (O'Connor *et al.*, 2014). Rising [CO₂] can accelerate woody plant growth through increasing available soil water through improving plant water-use efficiencies (Polley *et al.*, 1997; Leakey *et al.*, 2009), potentially extending the growing season, increasing maximum growth rates for individual woody plants while also increasing potential tree cover (where potential tree cover is not limited by other factors, e.g. soil fertility). Increased [CO₂] will also directly increase the rate of carbon uptake by plants, potentially increasing growth rates and the recruitment of woody plants (Bond & Midgley, 2000; Hoffmann *et al.*, 2000; Kgope *et al.*, 2010). The vulnerability of a region to encroachment will therefore depend on both the prevailing land use history, the environmental setting, as well as the functional traits of woody plants that likely govern their responsiveness to both local (e.g. sensitivity to fire) and global drivers (e.g. growth response to elevated [CO₂]). However, there are remarkably few experimental data examining the effect of increased [CO₂] on seasonally dry tropical vegetation and the plant functional types within them (but see (Hoffmann *et al.*, 2000; Stokes *et al.*, 2005; Kgope *et al.*, 2010).

These gaps in understanding highlight that there has been no systematic review of recent changes in woody cover that have occurred across savannas. While, the number of continental- and global-scale satellite studies of vegetation greenness are increasing, these studies cover only the short time-scale of the satellite record and record measures of greenness (e.g. NDVI) that incorporate the signal of both trees and grasses (Buitenwerf *et al.*, 2015; Liu *et al.*, 2015). We undertake a meta-analysis of studies documenting change in woody cover, with specific attention to studies of woody cover increase, across the tropical and sub-tropical savanna ecosystems of Africa, Australia and Brazil to assess the extent, magnitude and type of encroachment.

Materials and Methods

Data compilation

We conducted a meta-analysis of woody vegetation change in natural tropical and sub-tropical C4 grass-dominated savannas in Africa, Australia and South America. We defined savannas as C4 grasslands with a significant tree component following the definitions provided by Lehmann *et al.*, (2011) and Ratnam *et al.*, (2011). Sites were untransformed by large-scale agriculture, but could have been subject to livestock grazing. Studies documenting land clearing were excluded. We searched the literature using a combination of the following terms: “bush”; “woody”, “woody cover” “shrub”; “tree”; plus “thickening”; “encroachment”; “invasion”; “increase”; “change”; “dynamics”, “loss”, “mortality”, “decline”, “death”, “elephant damage”, “elephant impact”, “drought”, “wind fall”, “cyclone” and “storm”. Studies were included where woody cover, biomass or tree basal area was recorded at two or more points in time. These data were used to derive an annual increment of woody cover change, i.e. (final cover – initial cover) / time in years. Seven studies from the Brazilian cerrado were used where biomass or basal area was recorded. These values were converted to percent cover using a linear regression based on data from (Pinheiro, 2008). In Australia we used

converted measures of basal area to canopy cover using data presented by Lehmann *et al.* (2009). In Africa, similar conversion formulae were not available so only studies considering changes in woody cover were considered.

We also compiled studies documenting change in the extent of forest and savanna vegetation. Sites were included if they were untransformed by large-scale agriculture and human-induced afforestation or deforestation. The literature was searched using the terms, “forest”, “savanna”, “expansion”, “shift”, “increase”, “decrease”, “biome switch”. Similarly, these studies required two time points. However, across publications there was far less consistency in the metric of change quantifying changes in the extent of savanna. Change was recorded as both change in forest patch size (where the extent of an entire forest patch was measured) or the proportion of ground area covered by forest versus savanna over a given area. We therefore recorded changes as the proportional change of forest relative to savanna but did not use this in the statistical analyses described later.

From each study, we compiled site latitude and longitude, and used this information to compile climatic information from WorldClim (Hijmans *et al.*, 2005). Where possible, for each study by site combination we extracted information on the dominant land use at the site, the identity and basic traits of the encroaching woody plant species.

Uncleared savannas are dominated by three land uses; conservation and commercial and communal grazing land (predominately cattle grazing) (McAlpine *et al.*, 2009). Conservation lands represent the best control situation where natural disturbances caused by regular fires and moderate herbivory (grazers and browser) are mostly maintained. In some areas, elephants are

present, which can interact strongly with woody cover, by extensively damaging woody plants (Guldemon & Aarde, 2008). Commercial grazing is primarily centred around livestock production resulting in a grazer-dominated system (Scholes, 2009). In Africa, the other predominant land use is communally-owned subsistence farming (communal rangelands) (Scholes, 2009). In communal rangelands, communities rely on the land for natural resources and grazing. Where there was sufficient information provided, we assigned the site one of these predominant four land use types: conservation (without elephants); conservation (with elephants); commercial grazing; communal grazing. If the land was not used for any particular purpose it was termed remnant land. Where possible, we documented the main encroaching woody species at each site. If plants belonged to the family Fabaceae we recorded if the plants had the potential to fix atmospheric nitrogen (Sprent & Platzmann, 2001) (Appendix S4).

Statistical Analysis

Our database consisted of studies documenting both increases and decreases in woody cover over time (Figure 1). We found that studies that documented woody cover declines were often accompanied by direct evidence of the environmental driver of vegetation change (e.g. drought, elephant damage), and that these changes were generally observed over short time periods. Of the 110 sites in the database documenting savanna woody change, 13 sites documented declines in woody cover (Appendix S4). Of those sites, only two did not provide direct evidence for the cause of the decline. Therefore, we performed an analysis which aimed to investigate correlates of woody cover increase.

Data were analysed using a generalised linear model (Gaussian error family) framework in R (version 3.1.1) (R Core Team, 2014). We included initial woody cover as a covariate representing site level variation. Initial cover (IC) has an important bearing on the potential for a site to increase in

woody cover. We expect that sites low in woody cover are more likely to experience higher rates of woody cover increase simply because these sites are less limited by tree-tree competition, and where suppression of disturbance may facilitate rapid increases in woody cover closer to the potential (Roques *et al.*, 2001; Lehmann *et al.*, 2009). Continent was included as a factor given the observed regional differences in the functional relationships between woody vegetation and climate (Lehmann *et al.*, 2014). Further, based on the literature, it is clear that different human interventions have had more or less impact in different regions. Hence, continent could infer differences in both human management and ecological setting. Mean annual precipitation (MAP) was a covariate given that both mean woody cover and potential woody cover increase with MAP (Jolly *et al.*, 2005; Sankaran *et al.*, 2005; Lehmann *et al.*, 2014). Finally, we included the first year of a study to examine whether rates of cover change were constant through time. This could help infer whether global change drivers (i.e. [CO₂]) have relevance in interpretation of these data. We included an interaction between initial cover and continent as patterns of woody cover are also known to vary among continents. Unfortunately, we could not include other site level factors such as fire return time or herbivore abundance as these data were inconsistently recorded across studies. Given the variable time periods over which these studies were undertaken, it would be inappropriate to estimate a mean fire return time based on the more recent remotely sensed data.

Candidate models to describe rate of woody cover increase were compared using Akaike's information criterion, corrected for small sample sizes (AICc) to rank the models. As models with a $\Delta AICc < 2$ are considered well supported, we used model averaging on the models with a $\Delta AICc < 2$. We used the averaged final parameter estimates, standard errors and confidence intervals to demonstrate the effect size of the different parameters. All analysis was performed using the software R (version 3.1.1) (R Core Team, 2014) with the packages 'stats' and 'AICmodavg' version 2.0.3 for model selection and averaging. Following the full factorial model including continent we performed the same analysis for each continent separately. We did this to test the effect of variables, specifically

MAP, without confounding MAP and continent as the available rainfall range varies strongly between
continent (Lehmann *et al.*, 2011).

We tested for differences in the rate of woody encroachment between comparable land
uses within Australia and Africa using a one-way ANOVA. To test for differences in the rates of
woody cover between different land uses within Africa we used a two-way ANOVA. Post-hoc analysis
was performed using a TukeyHSD test in R (version 3.1.1) (R Core Team, 2014).

Results

Global patterns of woody cover change in C4 grassy ecosystems

Of 94 studies covering 110 savanna sites, woody encroachment was apparent in 84% of sites (Figures
1–2). Woody encroachment within savannas has occurred across the rainfall gradient in all three
regions (Figure 2a). Australia had the lowest average rate of woody cover change of 0.1% per year
(1% per decade) (Table 1), where only small net increases in woody cover were recorded (Figure 2b).
In Australia, 4 sites recording declines in tree cover were consistently attributed to inter-decadal
drought (Appendix 1, 4). Brazil had the highest mean rate of woody cover increase of 0.7% per year
(7% per decade) (Table 1, Figure 2b) with only 2 sites recording decreases in untransformed
savannas (Appendix 1,4). The average rate of increase in African savannas was 0.25% per year (2.5%
per decade) (Table 1, Figure 2b). Africa had the highest number of sites (14) documenting declines in
woody cover (Figure 2b), which were directly attributed to either elephants or inter-decadal
drought.

Twelve studies, covering 82 sites, examined forest expansion into savanna. Forest expansion
was recorded at 85% of sites examined (Figure 1, Table 1). In Australia, where the majority of sites

and studies occurred, forest expansion occurred at a rate of 0.7% per year (7% increase in forest area into savanna matrix, per decade) (72 sites). Here, forest expansion into savanna was usually attributed to fire suppression. There were significantly fewer studies of forest–savanna boundary shifts in Africa (5 studies) and Brazil (5 studies), forest expansion was still apparent across all sites. In Africa, a mean annual increase of 0.3% of forest area per year within the savanna matrix was observed, and in Brazil a larger mean annual increase of 1.1% forest area per year was recorded (Table 1).

We examined the relevance of continent, mean annual precipitation, start year and initial cover on rates of woody cover increase and identified two plausible models (Table 2a). Model averaged coefficients indicated that continent, mean annual precipitation, start year and initial cover had relevance in these data. Rates of woody cover increase were higher in studies which started later in the 1900s and early 2000s. We found a strong interaction between initial cover and continent, particularly in South America (Table 2b). There, annual rates of increase were highest with low initial woody cover, and thereafter the rate of annual increase in woody cover decreased as initial woody cover increased. We repeated this analysis separately for each continent. In Africa the start year was positively correlated with the rate of encroachment. In South America, observed rates increase were positively correlated with increasing the initial cover. Mean annual precipitation was not an important predictor of rates of woody cover increases in any of the continents.

African savannas can be classified into four land management types (Table 1 and methods). When comparing rates of woody cover increase among land management types, significant woody cover increases occurred across all of these management types except in conservation areas where elephants were present (0.1% per year) ($F_{3,49}=2.75$, $p<0.033$) (Table 1). A post-hoc Tukey test confirms that the presence of elephants is associated with significantly lower rates of increase in comparison to communal rangelands and grazed lands.

Contrasting patterns between continents

Cattle grazing is a land use common across Australia and Africa, enabling a comparison of woody cover changes across these comparable regions. We found that average rates of change in Africa were two and a half times of Australian savannas (2.5% vs. 1.1% per decade; Table 1), and the patterns of woody cover increase were significantly higher in African grazing land when compared to Australian grazing land ($F_{(1, 27)} = 16.04$, $p < 0.000$).

The biology of the encroaching species differed between continents. In Africa, 94% of sites (from the 71% of studies reporting such information) were characterised by species with the potential to fix nitrogen (Appendix S4). In South American savannas only 10% of sites were recorded as being characterised by N-fixing species (from the 85% of studies reporting such information). In Australia, none of the encroachment was caused by N-fixing species (from the 30% of studies reporting the dominant woody encroaching species).

Discussion

We demonstrate that woody encroachment – both within savannas and forest expansion into savannas – is widespread across the savanna biome. Woody encroachment, albeit with varying regional magnitude, occurred across regions and land uses. Our meta-analysis of historical records demonstrates a widespread trend of increasing woody cover, which was already apparent in the 1970s.

We found that initial cover was an important correlate of the rate of encroachment, where a high initial cover was associated with a lower subsequent rate of encroachment. This could potentially be attributed to density dependence (Roques *et al.*, 2001; Lehmann *et al.*, 2009). Mean annual precipitation was not correlated with the rate of encroachment in any region and encroachment occurred across the available rainfall gradient. Water availability is however a key constraint on savanna net primary productivity and maximum woody cover (Sankaran *et al.*, 2005; Staver *et al.*, 2011). It is therefore possible that unquantified site-level variation outweighed the role

of rainfall, or that this metric was insensitive to other water-related factors, such as duration of the dry season. Precipitation has been previously found to be an important correlate of encroachment, where in high versus low rainfall comparisons of encroachment, sites at high rainfall are more likely to fluctuate in woody cover over time (Lehmann *et al.*, 2009). Continent was an important correlate of the rate of encroachment where Brazilian savannas have experienced, on average three times the rate of encroachment of African savannas and seven times the rate of Australian savannas. Local differences in fire and browse history, soil nutrient status and physical structure could not be consistently quantified in this analysis as this information was not consistently reported.

Extensive encroachment across savannas could suggest a uniform global driver of change, specifically elevated [CO₂] that has been variously hypothesised to drive a re-organisation of tropical vegetation. However, our correlative analyses do not preclude regional and local drivers of change generating similar net effects. Therefore, a more compelling approach to test for evidence of a global driver is to examine encroachment across land uses which are expected to have different trends in woody cover over time. In Africa, three land uses are common to untransformed savannas; commercial cattle ranches, communal rangelands and conservation areas. Commercial cattle farming causes a grazer (cattle) dominated system characterised by a moderate but constant stocking rate with an infrequent fire return period (Higgins *et al.*, 1999; Roques *et al.*, 2001). Encroachment is often predicted for this land use type (Wigley *et al.*, 2010). In contrast communal rangelands, subsistence agriculture around rural villages, are predicted to experience declines in woody cover due to wood harvesting for building, energy and income (e.g. charcoal). Rates of woody cover decline are predicted to increase as human densities increase (Banks *et al.*, 1996; Ryan *et al.*, 2014). The third land use is conservation, where little change in woody cover is predicted due to regular fires and moderate herbivory (grazers and browsers) maintaining savanna ecosystems. A common distinction within conservation areas is the presence or absence of elephant, the presence of which is predicted to cause declines in woody cover (Guldmond & Aarde, 2008). Our analysis

demonstrates that within Africa encroachment has occurred across all these land uses, except in the presence of elephants. This is a powerful indicator that in Africa a global driver is a likely cause of woody encroachment and also highlights the role of mega-herbivory in slowing encroachment. Indeed, the contrast between areas with and without elephants (Table 1) highlights that the removal of elephants is also a likely significant cause of encroachment across Africa (Guldemond & Aarde, 2008), as free-roaming elephants have disappeared from many parts of Africa and are now largely confined to conservation areas (Owen-Smith, 1992). In contrast, the mega-herbivore fauna of Australia and Brazil have been extinct for millennia, such that the legacy will not be evident in contemporary trends of vegetation change.

A second indicator for a global process is how rates of encroachment vary with time. We found that in Africa, the later the start year the higher the rate of encroachment. For example, a 10-year study starting in 1960 ending in 1970 was likely to have a lower rate of encroachment than a study starting in 1995. Accelerating encroachment rates have been noted in other African studies (Buitenwerf *et al.*, 2012; O'Connor *et al.*, 2014). This is congruent with the encroachment rates responding to an increasing intensity of a global driver, most likely increasing atmospheric [CO₂], increasing land-use intensity and increasing disruption of fire and mega-herbivory (Ramankutty & Foley, 1999; Archibald *et al.*, 2013).

What is the role of continent?

Encroachment is occurring across all savannas, however the regional context appears linked to observed rates of encroachment. This highlights that regional specific characteristics such as land use and the biology of flora is required to contextualise our findings. For example, human intervention in the contiguity of savannas has been severe in the Brazilian cerrado (Klink & Machado, 2005) and the extraordinary rates of encroachment across Brazil appear a direct consequence of a legislated policy of fire suppression (Klink & Machado, 2005). Fire extent and frequency are further

reduced by landscape fragmentation and transformation with only a few savanna patches larger than 1000 ha remaining (Durigan *et al.*, 2003; Klink & Machado, 2005; Silva *et al.*, 2008). Therefore, in Brazil the net impact of local processes is likely causing encroachment at a regional scale across remaining Brazilian savannas.

In Africa, savanna encroachment is significantly higher than that observed in Australia. These differences are more pronounced (2.5 times higher) when comparing similar land uses (commercial cattle ranching). Our findings point to a global driver, most likely elevated [CO₂], in African savannas even though this region also has the most records of woody cover declines. Elephant impacts and low soil nutrients, harvesting pressures by humans were instrumental in causing these observed reductions in woody cover particularly in the nutrient poor *Brachystegia* dominated savannas (Mapaure & Campbell, 2002; Ryan *et al.*, 2014). These observations raise the question, what makes Australian savannas relatively resistant to woody encroachment, particularly when no regional land use or policy can explain the changes?

Australian savannas are characterised by low nutrient soils, highly connected landscapes with little topographic barriers that generate fire regimes of frequent, intense and large fires (Archibald *et al.*, 2013). Frequent fire retards tree growth, biomass and establishment (Murphy *et al.*, 2014) and could buffer encroachment in landscape that has densities of less than 1 person per km² (Australian Bureau of Statistics, 2012). Whilst there are regional differences within Australia in both rainfall seasonality and fire regimes (Archibald *et al.*, 2013), Australian savannas generally have extreme seasonality and longer dry seasons than either Africa or Australia (Lehmann *et al.*, 2011; Staver *et al.*, 2011). Although reduced evaporation and improved water use efficiencies from [CO₂] fertilisation could act to increase the duration of the growing season (Donohue *et al.*, 2013), the effect is potentially small, relative to other savanna regions as the dry season remains in excess of six months and will still result in seasonal drought and fire.

In contrast with Australia and Brazil, African savannas contain a high abundance of nitrogen-fixing woody plant species from the family Fabaceae (Appendix S3). Their dominance could enhance ecosystem level responses to elevated [CO₂] (Leakey *et al.*, 2009) as nitrogen-fixing species can match the elevated rates of photosynthesis with increased nitrogen-fixation (Rogers *et al.*, 2009a) by producing more nitrogen-fixing tissues (Leakey *et al.*, 2009; Rogers *et al.*, 2009a), or a greater nitrogenase activity. Additionally, improved water use efficiencies associated with elevated [CO₂] could lower drought inhibition of nitrogen-fixers (Polley *et al.*, 1997; Rogers *et al.*, 2009b). The role of nitrogen-fixing species in savanna ecology has generally been ignored despite the dominance of these taxa in African savannas. With elevated [CO₂] and/or reduced drought stress, communities with a high proportion of nitrogen-fixing woody species may display rapid increases in biomass over time.

Regional variation in plant architecture occurs between savannas of Africa, Australia and South America (Dantas & Pausas, 2013; Moncrieff *et al.*, 2014). Regional differences in stem diameter to canopy diameter ratios must change the rate at which tree cover increases per unit of carbon gain. For example, Australian savanna trees are characterised by tall narrow canopies when compared to African savanna trees which have, on average, canopy widths twice that of Australian trees for a given stem diameter (Moncrieff *et al.*, 2014). These architectural differences are likely to result in different rates of encroachment, for example an increase in woody cover from 20% to 40% would require more than twice the carbon gain in Australia as Africa (Moncrieff *et al.* 2014). Therefore, all else being equal, the architectural traits of African savanna trees will promote higher rates of woody cover increase in African than Australian savannas.

Finally, African savannas are dominated by deciduous woody species (Chidumayo, 2001; Bowman & Prior, 2005). In deciduous savanna systems [CO₂] mediated increases in water use efficiency could extend the growing season by alleviating moisture limitation at the beginning or the

end of the growing season. An extended growing season, where leaves are retained for longer periods, has already been recorded in some semi-arid African savannas (Buitenwerf *et al.*, 2015). A delay in leaf fall in the early dry season, when average daily temperatures remain moderate, would extend the photosynthetically active period for plants (Stevens *et al.*, 2015). In contrast, both Australian and Brazilian savannas are dominated by evergreen woody plant species and changes may be relatively less pronounced (Bowman & Prior, 2005; Buitenwerf *et al.*, 2015).

Gaps and bias in the literature

This review highlighted notable gaps in information. Across Africa, the *Brachystegia* dominated savannas cover 2.7 million km² (Pienaar *et al.*, 2015) (similar expanse to all Australian savannas) yet there is a paucity of studies in this region. In South America, we could find only 2 studies documenting woody cover across Venezuelan savannas. On the other hand, other regions were over represented, generating a spatial bias within the dataset, most notably in South Africa. Additionally a publication bias almost certainly exists where studies which do not document either positive or negative change are less likely to be published.

Conclusions

Encroachment is occurring across the savanna biome. Our results demonstrate that these patterns and their potential causes are not easily extrapolated across savanna regions and that regional context is key to interpretation of these trends. Savannas regions are dominated by different plant families with different suites of biological traits (Lehmann *et al.* 2014). We argue that the biology of regional floras will influence the susceptibility of a region to encroachment. While, our study allows us to chart trajectories of woody cover change it does not allow us to determine the underlying causes of encroachment. However, this comparison enables us to establish testable hypothesis to explain regional variation in encroachment, highlighting the need for experimentation that to date has been lacking in savanna ecology.

384

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389 **Author contributions**

390 NS and CL conceived the study, analysed the data and wrote the paper. NS, CL, GD and BM compiled
391 the data, and GD and BM provided comments on a draft of the manuscript.

392

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Table 1: Summary of woody cover change studies across savannas and forest–savanna boundaries separated by continent and land use.

	No. data points	Mean duration (years)	Mean starting year	Mean change in woody cover (%)	Mean rate of change (% year ⁻¹)	Mean initial woody cover (%) or % forest cover
African forest–savanna	5	34	1962	8.5	0.3	14.3
African savanna	68	68	1948	10.8	0.25	20.1
Subsistence grazing land (communal)	25	62	1941	10.6	0.13	20.4
Conservation (without elephants)	6	46	1953	16.5	0.4	23.4
Conservation (with elephants)	19	33	1962	3.2	0.3	33.6
Grazing	17	58.4	1941	17.2	0.3	13.1
Australian forest– savanna	72	42	1961	27.3	0.7	Not reported
Australian savanna	18	45	1951	4.7	0.1	20.3
Conservation	1	40	1964	4.9	0.1	62.7
Grazing	17	45	1951	4.7	0.1	17.0
S. American forest– savanna	5	10	2002	7.5	1.04	59.8
S. American savanna	19	18	1984	16.3	0.74	42.4
Conservation	10	13	1994	4.8	0.43	60.3
Grazed	9	23	1973	29.2	1.1	20.0

Table 2a: Best models (where $\Delta AIC_c < 2$) assessing the relationship between variables and the annual rate of woody cover increase (% yr⁻¹). Models are ranked based on differences in the corrected Akaike's Information Criterion (ΔAIC_c). K is the number of estimated parameters, Akaike weight ($AIC_c Wt$) is the weight of each model. AC = annual rate of change; CONT = continent; SY= starting year, IC = initial cover; T = duration; MAP = mean annual precipitation.

Model	K	ΔAIC_c	$AIC_c Wt$	% deviance explained
AC ~ CONT +MAP+SY+ IC + IC:CONT	9	0.00	0.51	17.7
AC ~ CONT+MAP+IC+IC:CONT	8	0.67	0.36	18.32

Table 2b .Final parameter estimates (β), standard errors (SE) and confidence intervals of model averaging based on top models (see Table 2). Significant parameters i.e. where confidence intervals do not overlap zero, are show in bold. SY = Starting year, AC = annual rate of change; CONT = continent; IC = initial cover; MAP = mean annual precipitation.

Predictors	β	Lower CI (2.5%)	Upper CI (97.5%)	SE
Intercept	-5.1246	-16.6910	6.4417	5.8590
SY	0.0027	-0.0007	0.0099	0.0030
IC	0.0035	-0.0021	0.0091	0.0028
MAP	0.0004	0.0000	0.0008	0.2639
CONT (Aus)	-0.2190	-0.7443	0.3064	0.3122
CONT (S Am)	0.8764	0.2549	1.4978	0.0002
CONT (Aus): IC	-0.0032	-0.0135	0.0070	0.0051
CONT (S Am):IC	-0.0182	-0.0286	-0.0079	0.0052

Table 3 .Final parameter estimates (β) and standard errors (SE) from a GLM performed separately for each continent. Significant parameters are in bold.

	Africa	Australia	South America
Intercept	-12.83/5.930	-1.703/2.483	23.97/20.42
Start Year	0.006/0.003	0.0009/0.0013	-0.0113/0.011
Start cover	--0.0004/0.0002	-0.0009/0.0005	-0.0132/0.0056
MAP	-0.000/0.0001	0.0000/0.0001	0.0000/0.0012

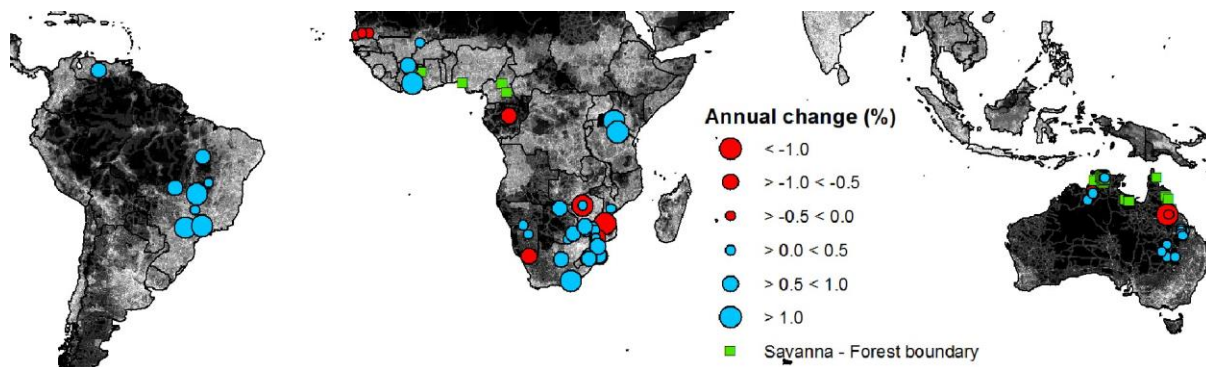


Figure 1: Sites with reported change in woody cover in tropical C4 grassy ecosystems. Blue circles indicate savanna woody encroachment. Red circles indicate a decline in savanna woody cover. The size of the circle reflects the magnitude of the rate of change in woody cover relative to the duration of the study. Green squares indicate locations where forest expansion into savannas has been reported. Due to the variability in the methods of measurement for change in forest–savanna boundaries, we only denote change without showing the magnitude of change. The background map shading represents the human impact index (HII), where darker shading represents less intervention in the landscape, and lighter shading a higher human impact. The scores provided by the HII range from 0 to 100, and combines socio-economic, roads, land tenure and data on land transformation (Sanderson *et al.*, 2002). Due to the nature of the symbols not all symbols are visible (e.g. forest–savanna boundary change in South America). Please see published database for all records (Appendix S1 & S2).

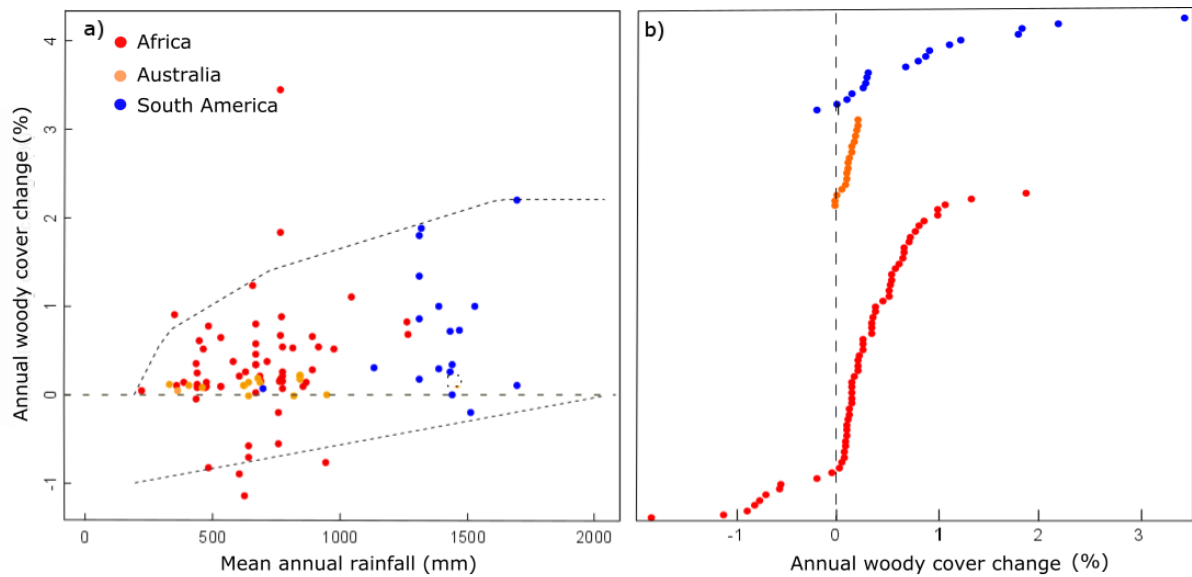


Figure 2a: Annual rate of woody cover change plotted against mean annual rainfall. Upper and lower dashed lines represent the 5th and 95th percentiles. Positive values indicate woody cover increases whilst negative values indicate decreases **b)** Annual rate of woody cover change for each site, shown in rank order. Points are separated by continent in Africa (red), Australia (orange) and South America (blue). The dashed vertical line marks the divide between increases and decreases.